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ANATOMICAL NOTES ON *LUTODRILUS MULTIVESICULATUS* (ANNELIDA: OLIGOCHAETA)[1]

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Abstract.—Anatomical studies of specimens of *Lutodrilus multivesiculatus* McMahan, 1976, demonstrate the uniqueness of the species and of its monotypic family Lutodrilidae among the oligochaetes. Features conspicuously different from those of other megadrile taxa include the arrangement of the parietal musculature, the large number of metameres containing male reproductive structures, and a vascular system that includes eleven pairs of hearts and caudal subcuticular capillary beds.

The description of *Lutodrilus multivesiculatus* McMahan, 1976, placed this megadrile into a monotypic genus and family, the Lutodrilidae. Subsequent to the description, more extensive anatomical studies of the species have been completed.

External Anatomy

Secondary furrows are present anterior to xxi–xxiv, and tertiary furrows begin in vii, occurring posteriorly to xiv–xxiv. Each type of intrasegmental furrow is most evident dorsally. Body shape is almost circular in anterior cross section and is quadrangular posteriorly, beginning approximately at vii. The quadrangular shape is most pronounced posterior to gonadal segments, with setal couples at the 4 angles of the body. Setal arrangement is lumbricin, with setae closely paired in a slightly postequatorial position. Setae are curved distally and have jagged, transverse ridges immediately proximal to the curved portion. A nodulus is one-third of the setal length from the distal tip. In nonregenerates, the tip of the tail often is reflected over the posterior border of the anus. Nephropores are inconspicuous, identifiable only in histological sections.

The clitellum is annular and only slightly swollen, with indistinct anterior and posterior margins. The body in this region is compressed dorsoventrally, and the ventral surface is flattened or concave. The extent and location of the clitellum are variable, as indicated in Table 1. Intraclitellar

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Table 1. Location of clitellum in *Lutodrilus multivesiculatus*.

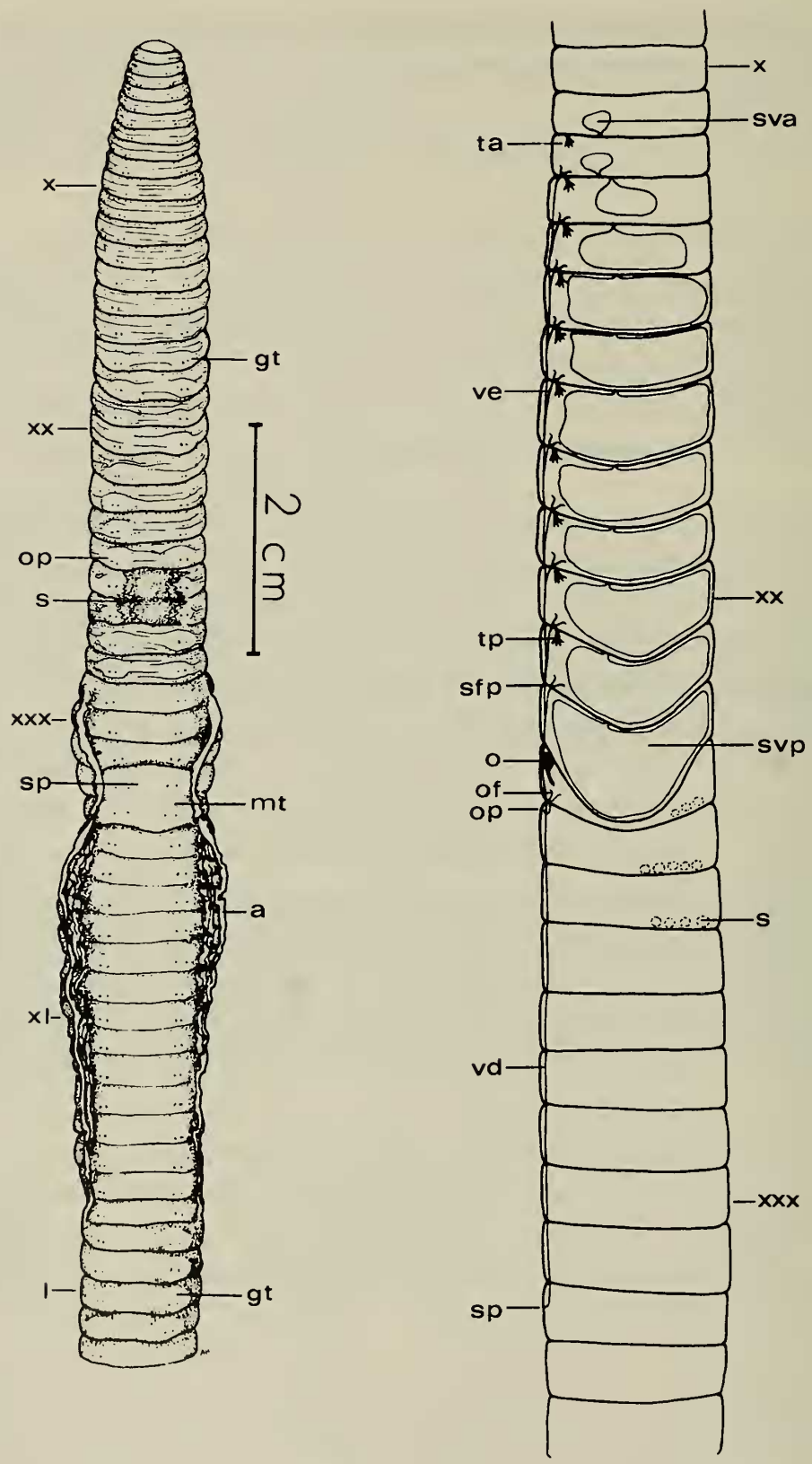
Segments included	Number of segments	Number of specimens
xx–lxvi	47	1
xxi–lxiv	45	1
xxi–lxvi	46	1
xxi–lxviii	48	1
xxi–lxxi	51	1
xxii–lxv	44	1
xxii–lxvi	45	1
xxv–lxi	37	1

intersegmental furrows are not obliterated by clitellar development. The clitellum is multilayered dorsal to the alae only, not extending onto the ventrum; however, the coloration is annular with the exception of the genital tumescences and ventral surfaces of the alae, both of which are white to tan in contrast to the reddened coloration of the clitellum.

The tubercula pubertates include 16–32 segments, xxii–liii (Table 2), are aliform, and extend 1.5 mm from the body in preserved material and 2–3 mm in living animals (Fig. 1). The alae originate lateral to *B* and in life are flared laterally. Genital tumescences are small, rounded elevations not sharply demarcated from the surrounding epidermis (Fig. 1). Each tumescence surrounds and includes 1 ventral setal pair, and the tumescences are superficial, being totally extramuscular. Each of segments xiii–xxx, usually xvi–xxviii, and xxxiv–lii may possess 1, 2, or no tumescences, each limited to the region around *a,b* (Tables 3 and 4). Frequently, genital tumescences

Table 2. Location of alae in *Lutodrilus multivesiculatus*.

Segments included	Number of segments	Number of specimens
xxii–li	30	1
xxii–liii	32	1
xxvii–xlii	16	1
xxviii–xlix	22	1
xxviii–l	23	1
xxviii–li	24	2
xxix–xlvi	18	1
xxix–xlviii	20	1
xxix–xlix	21	2
xxix–l	22	3
xxix–li	23	3
xxx–xlvi	17	2
xxx–li	22	1



Figs. 1–2. *Lutodrilus multivesiculatus*. **1** (left), Anterior end of clitellate specimen of *Lutodrilus multivesiculatus*, ventral view. **a**, ala; **gt**, genital tumescence; **mt**, male tumescence; **op**, location of oviducal pore; **s**, spermatophore; **sp**, location of spermiducal pore. **2** (right), Diagrammatic longitudinal section of genital region, not drawn to scale. **o**, ovary; **of**, oviducal funnel; **op**, oviducal pore; **s**, spermatheca (spermathecae illustrated in only 3 intersegmentals); **sfp**, posteriormost spermiducal funnel; **sp**, spermiducal pore; **sva**, anteriormost seminal vesicle; **svp**, posteriormost seminal vesicle; **ta**, anteriormost testis; **tp**, posteriormost testis; **vd**, vas deferens; **ve**, vas efferens.

Table 3. Distribution of genital tumescences in *Lutodrilus multivesiculatus*

First and last segments of series	Number of segments	Number of specimens
xiii–lii	40	1
xv–li	37	1
xvi–xlviii	33	1
xvi–xlix	34	2
xvi–li	36	2
xvi–lii	37	2
xvii–li	35	2
xvii–lii	36	1
xviii–li	34	1
xix–li	33	1

are absent on most or all of segments xxxiv–xlvi. In clitellate individuals, genital tumescences are white to tan in contrast to clitellar coloration whereas, in aclitellates, the color of the genital tumescences is like that of the surrounding epidermis. The male tumescence is an elevated, flattened area on the ventrum of xxxii–xxxiii, sometimes extending onto portions of xxxi and/or xxxiv (Fig. 1). The male tumescence contacts the alae, thus including both ventral setal couples of each segment. The ventral setal pairs of xxxi–xxxiv are displaced medially. In xxxi and xxxiv, the amount of displacement is equal to half of *AB* whereas *b* of xxxii and xxxiii is in the *A* line of segments other than xxxi–xxxiv (Fig. 1). Spermathecal pores are minute, unrecognizable macroscopically, and are multiple in each intersegmental 15/16–25/26, ventral to *C*.

Internal Anatomy

Musculature

Septa are present posteriorly beginning with 3/4 and are thickened and heavily muscularized 7/8–23/24. Posterior to the pharynx, septa are markedly depressed posteriad. Muscles extend from the pharynx to parietal insertions, ending in vii.

Anteriorly, the body wall is distinctive, being ca. 1.5 mm thick in ix of a mature specimen and having 5 distinct muscle layers: subepithelial circular, diffuse longitudinal, median circular, trabeculate longitudinal, and retroperitoneal circular (Fig. 3). The median circular muscle layer diminishes posteriorly and ends in xviii. In midbody, the body wall is ca. 0.75 mm thick, and there are 3 muscle layers: 2 circular layers with a median trabeculate longitudinal layer (Fig. 4). The retroperitoneal circular layer is much thinner than anteriorly. Near the periproct, the body wall musculature is much

Table 4. Pattern of distribution of genital tumescences of 3 specimens of *Lutodrilus multivesiculatus*.

Segment	Position on segment 1	2	3
pre-xv	none	none	none
xv	right	none	none
xvi	left	bilateral	none
xvii	bilateral	left	none
xviii	bilateral	right	left
xix	bilateral	right	none
xx	bilateral	left	right
xxi	bilateral	bilateral	bilateral
xxii	bilateral	bilateral	right
xxiii	bilateral	bilateral	right
xxiv	bilateral	bilateral	bilateral
xxv	bilateral	bilateral	bilateral
xxvi	bilateral	bilateral	bilateral
xxvii	bilateral	none	bilateral
xxviii	bilateral	none	left
xxix	right	none	none
xxx	bilateral	none	none
xxxi	bilateral	none	right
xxxii	male tumescence	male tumescence	male tumescence
xxxiii	male tumescence	male tumescence	male tumescence
xxxiv	bilateral	none	none
xxxv	none	none	none
xxxvi	none	none	none
xxxvii	right	none	none
xxxviii	left	none	none
xxxix	none	right	none
xl	none	none	none
xli	left	none	none
xlii	none	none	none
xliii	none	none	none
xliv	none	none	none
xlv	none	none	none
xlvi	none	none	none
xlvii	bilateral	bilateral	none
xlviii	bilateral	bilateral	right
xlix	right	right	none
l	right	none	none
li	right	none	bilateral
lii and following	none	none	none

reduced. The only distinct layer is the outer circular muscle, beneath which is a loosely arranged layer of longitudinal fibers that are not organized into well-defined bundles. Immediately internal to the peritoneum, there is a muscle layer consisting of 1 to 2 thicknesses of circular muscle fibers.

In megadriles, the existence of distinct circular muscle layers other than immediately subepidermal in position is unknown. Such a condition would be expected to accompany reduction of the outermost layer of circular muscle; however, this is not the case. To the contrary, in *L. multivesiculatus*, the outermost circular muscle layer is thickest anterior to and including x—the part of the body in which the 2 inner circular layers are best developed. The proportional amount of circular muscle in this region is greater than in any other known megadrile and, comparatively, results in an extremely powerful probing capability with the anterior segments.

The retroperitoneal circular layer, always present throughout the body, is thickest anterior to x, posterior to which it diminishes to equal the thickness of the outermost circular layer. Near the periproct, the retroperitoneal circular musculature is one-sixth of the thickness of the subepidermal layer.

The trabeculate muscle layer is most highly developed in the region of xii, where it is ca. 1.2 mm thick. "Kästchen" are poorly defined, and they lack discernible internal organization. Fibers within a "kästchen" are arranged into small, randomly distributed bundles that are most dense ectally. Fascicles of connective tissue occasionally infiltrate between the bundles. This arrangement resembles that reported in *Eisenia foetida* (Savigny) and *Allolobophora chlorotica* (Savigny) by Harman (1960) although it is less organized than in either of these 2 species.

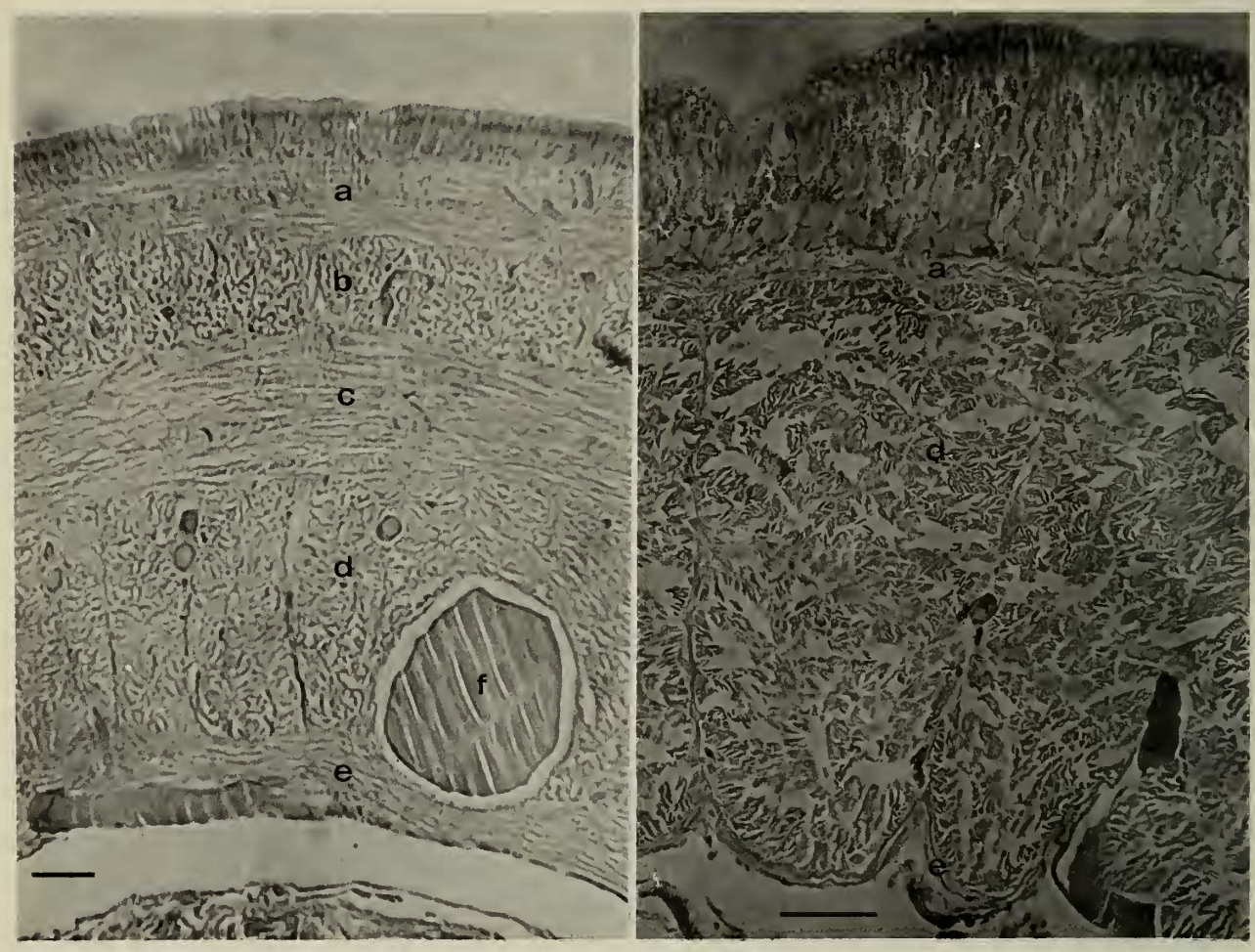
The outer longitudinal muscle layer consists of small, diffuse bundles of fibers that only occasionally are enclosed by connective tissue fascicles. The radial fascicles of connective tissue separating "kästchen" of the trabeculate layer sometimes penetrate the median circular layer and pass through the outer longitudinal layer, dividing its fibers into ill-defined bundles.

Nervous System

The brain, located in ii–iii, is bilobed and gives rise to 2 circumpharyngeal commissures at 2/3. Each commissure is one-third the diameter of the single ventral nerve cord, which the commissures join in iii. Five pairs of nerves branch anteriad from the brain: 2 to the roof of the buccal cavity and 3 to the prostomium, peristomium, and parieties. Segmentally, 3 pairs of lateral nerve trunks arise from the nerve cord.

Digestive System

The digestive tube lacks crop, gizzard, and calciferous glands. The pharynx is in ii–vi, with muscle fibers to the parieties extending to vii. An esophageal valve originates from the dorsal wall of the esophagus in vii. The esophageal mucosa becomes folded longitudinally in xvi, with vascular sinuses in xvi–xx. The gut widens at 20/21, and intestinal pouches begin in



Figs. 3–4. *Lutodrilus multivesiculatus*. **3** (left), Cross section of anterior body wall; **4** (right), Cross section of body wall in clitellar segment. **a**, subepithelial circular muscle; **b**, diffuse longitudinal muscle; **c**, median circular muscle; **d**, trabeculate longitudinal muscle; **e**, retroperitoneal circular muscle; **f**, lateroparietal vessel. Scales 100 μm.

xxi–xxiv, extending to the region of 1. Each pouch, a dilatation of the intestine, is variable in length, extending up to 10 segments. The dorsal typhlosole begins as a low proliferation of tissue in xxxi–xxxiv and may obliterate the intestinal lumen posteriorly. The peduncle of the typhlosole is nearly as broad as the distal portion (Fig. 5). Chloragogen is present from the anterior segments, with greatest accumulations in xx and succeeding segments.

Nephridia

Nephridial tubules extend into the upper part of the coelom and adhere closely to the parieties. Nephrostomes are single.

Genitalia

Seminal vesicles are largest in xiv–xxii, where they often fill the coelom to the middorsal line (Fig. 2). Vesicles are attached to the posterior faces

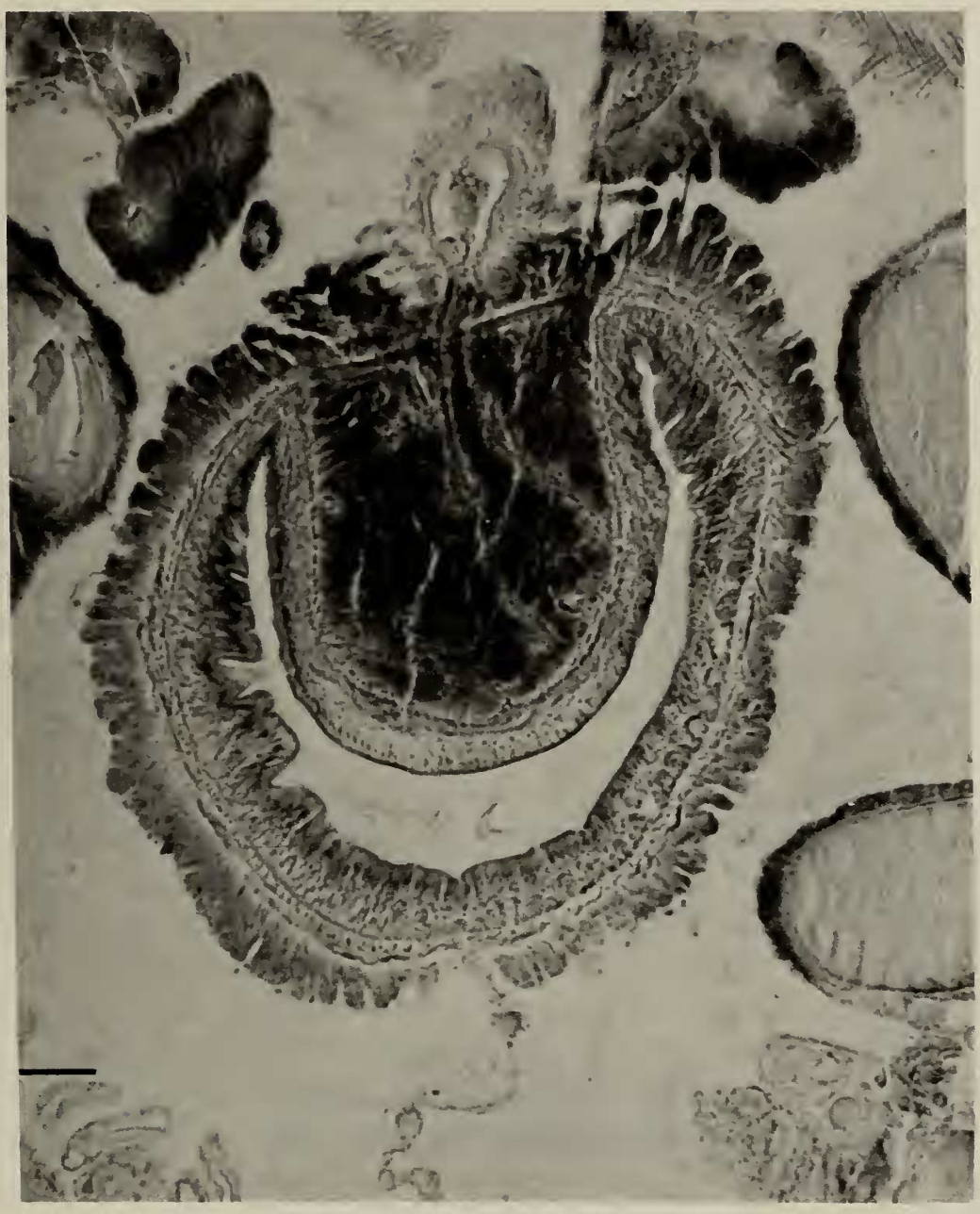


Fig. 5. Cross section of typhlosolar intestine of *Lutodrilus multivesiculatus,* scale 100 μm.

of their respective septa with the exception of the vesicles of xi and xii, which attach to the anterior faces of septa 11/12 and 12/13, respectively. Testes are digitate, ending distally in numerous strings. The large, polyplicate spermiducal funnels surround ventrolateral portions of the seminal vesicles. The vasa efferentia are microscopic, having diameters of 50–75 μm. They enter the parieties one segment posterior to their respective funnels and orient posteriorly in a retroperitoneal position. One, or sometimes 2, segments posterior to their origins, the vasa efferentia join the intramuscular vasa deferentia, which also are microscopic (ca. 75 μm in diameter). The vasa deferentia are embedded in the trabeculate longitudinal muscle layer approximately half the distance through the body wall; however, they move toward the coelom at the junction with each vas efferens. Each vas deferens

is lateral to *B* until 31/32, where it begins medial orientation through the ventral parieties toward the spermiducal pore in xxxii. Prostates are lacking.

Each mature ovary resembles a rounded triangle with a posterior apex tapering to a single egg string containing 6–10 maturing oocytes that are visible through the ovarian wall (Gates, 1976; McMahan, 1976). Immature ovaries lack the egg string although developing oocytes are visible through the wall of the ovary (Gates, 1976). The crenellate oviducal funnels are smaller than and more closely attached to the septum than are the spermiducal funnels. Oviducts pass posteriorly through septum 23/24, which is depressed posteriad by the seminal vesicles of xxii, and the ducts then orient anteriad toward their entrance into the parieties lateral to *B* and presetal.

Spermathecae are ovoidal, averaging ca. 150 × 200 × 275 μm, and are intraparietal in the outer layer of longitudinal muscle in intersegmentals 15/16–25/26. Spermathecal number varies, 2–5, on each side of a segment, and these structures often are not paired bilaterally. Spermathecae are ventral to *C*. Thecal ducts are simple, adiverticulate tubes ca. 90 μm in diameter and 150–300 μm in length leading to superficial pores in the intersegmental furrows.

Epidermal glands are associated with the ventral setae of xxii–xxvii. One acinar gland is associated with each of setae *a* and *b*, posterior to the seta. Glands are limited solely to the epidermis, and straight ducts open on a slight surface elevation.

Vascular System

According to Gates (1970), the artificiality of the classical system of oligochaete systematics, as rendered in *Das Tierreich*, Vol. 10 (Michaelsen, 1900) and later supported by Stephenson (1930), was due largely to unwarranted emphasis of reproductive structures and lack of attention to somatic structure. Gates (1962) determined that vascular features provide diagnostic characteristics for natural taxa, perhaps to the familial level. Brinkhurst (1971) stated that the potential value of the vascular system in oligochaete systematics is not fully utilized due to inadequate knowledge concerning many taxa. Recent papers devoted exclusively to vascular system studies (e.g. Johansen and Martin, 1965; Righi, 1972; Righi and Bittencourt, 1972) reaffirm the significance of this system. Because of the uniqueness of the vascular system in *Lutodrilus multivesiculatus*, a comprehensive discussion of this system follows.

The vascular system is described from 3 regions of the body: (1) anterior to xxiii, where much differentiation occurs due to cephalization; (2) intestinal segments, where vascular elements are metameric; and (3) the preperiproct region, where there is extensive parietal vascularization. Nomenclature of the vessels follows that of Righi (1972), with modifications.

ANTERIOR TO XXIII.—There are 4 primary longitudinal vascular trunks anteriorly: the ventral and dorsal vessels and a pair of lateroparietal vessels. Less prominent longitudinal vascular features are subneural sinuses and a pair of latero-esophageal vessels.

Ventral vessel.—This vessel, continuous throughout the body, undergoes a great decrease in diameter anterior to v. In iv, the ventral vessel bifurcates, and each branch circles the pharyngeal bulb near the circumpharyngeal nerve commissure. Many branches of the circumpharyngeal vessels vascularize the pharynx, brain, commissures, and body wall of the first 3 segments.

Dorsal vessel.—This trunk begins at septum 10/11 and follows a sinuous path along the dorsum of the alimentary tract. Anterior to its juncture with heart xi, the diameter of the dorsal vessel is very small, and it is disjunct from the digestive tract and surrounded by chloragogue. The size of the vessel increases to heart xiv, behind which it is uniform except for septal constrictions. Two pairs of dorso-intestinal vessels extend from the dorsal vessel to the esophagus segmentally posterior to x.

Lateroparietals.—These bilaterally-paired vessels, present anterior to 22/23, are located slightly lateral to *B* and are retroperitoneal or immediately external to the innermost layer of circular muscle (Fig. 3). In iii, they terminate by forming circumferential vessels that branch to capillarize adjacent portions of the parieties and digestive tract. Segmentally, the lateroparietals give rise to large retroperitoneal circumferential vessels with radial branches passing through the longitudinal muscle to vascularize the outer body wall. In xxii, the lateroparietals cross the coelom and join the dorsal vessel at 22/23. In the coelom of xxii, each lateroparietal gives rise to a large branch to the subneural vessel, which greatly increases in diameter posterior to this point.

Subneural vessel.—Although the subneural vessel is not continuous anterior to xxii, a succession of sinuses, 2–3 per segment, is present in that region. Each of these sinuses, present in iv–xxii, originates by the union of capillaries within the neural sheath, vessels from the parieties, and a branch from each latero-esophageal, and the sinuses lose their identity in a similar fashion. Their position within the neural sheath is identical to that of the subneural vessel, which is not continuous until xxii, where it receives a large connective from each lateroparietal vessel.

Latero-esophageal vessels.—The pair of latero-esophageals originate from capillaries on the pharyngeal dorsum in ii. They enlarge while on the dorsum of the pharyngeal mass and begin to orient ventrally around the pharynx in vi. In vii, they join smaller trunks that form ventrolaterally on the pharynx. Posterior to vii, the latero-esophageals, surrounded by chloragogen, are positioned ventrolaterally on the alimentary tract; therefore, they differ from extra-esophageals, which are free from the esophagus for

much of their length and are more ventral with respect to the digestive tract than are latero-esophageals (Righi, 1972). Anterior to each septum 7/8–12/13, there is a large connective from each lateroparietal to the latero-esophageals, which also receive branches from the alimentary tract and subneural vessels. In ix, there is a pair of connectives from the dorsum of the gut to the latero-esophageals, which terminate posteriorly by capillarization in the seminal vesicles of xii, immediately after branching to the lateroparietals.

Hearts.—The most conspicuous vascular features anteriorly are the 11 pairs of hearts, 1 pair segmentally in xi–xxi. Only 8 pairs, in xiv–xxi, are highly contractile whereas those of xi–xiii are smaller and are easily mistaken for commissural vessels. Every heart is muscularized, contains up to 8 valves, and enters the ventral vessel. Hearts are lateral, i.e. connecting the dorsal and ventral vessels; however, the junction of the heart and ventral vessel is not the primary route for blood in xi–xv. In each of these 5 segments, there is a large ventrolateral branch from the heart to the parieties that eventually enters the lateroparietals. Such branches are termed ventrotegumentary vessels and are known from several megadrile genera (Perrier, 1881; Bourne, 1891; Righi, 1972). Hearts of xi–xv have very small diameters (ca. 25 μm in xi) as they enter the ventral vessel; therefore, anteriorly, the major afferent vessels are the lateroparietal vessels because they receive blood from the first 5 hearts.

Intestinal Region.—In intestinal segments posterior to xxiii, there are 3 longitudinal trunks: dorsal, ventral, and subneural. Constrictions at the septa occlude the lumens of all 3 vessels. Vascularization is metameric.

Dorsal vessel.—The dorsal vessel, the efferent trunk, is embedded within the chloragogue on the intestinal dorsum and receives 3 pairs of vessels per segment: a pair of commissural vessels and 2 pairs of dorso-intestinal vessels. The commissural vessels penetrate the posterior septum to carry blood from the posteriorly adjacent segment to the dorsal vessel. There are 5 tributaries of each commissural:

a) Ventroseptal vessel. Each commissural vessel originates in the ventral septum from numerous capillaries that coalesce to form the ventroseptal vessel, which therefore drains the ventral portion of the septum.

b) Ventroparietal vessel. This vessel drains the ventrolateral body wall, where it originates as numerous smaller vessels draining the parieties. The union of the ventroparietal and ventroseptal vessels creates the ventral extremity of the commissural vessel, which courses dorsally a considerable distance before receiving the next efferent trunk, the lateral septoparietal vessel.

c) Lateral septoparietal vessel. Two small blood vessels arise in the lateral parieties and unite to give rise to the lateral septoparietal vessel. While coursing across the septum, this vessel receives many capillaries from the septum.

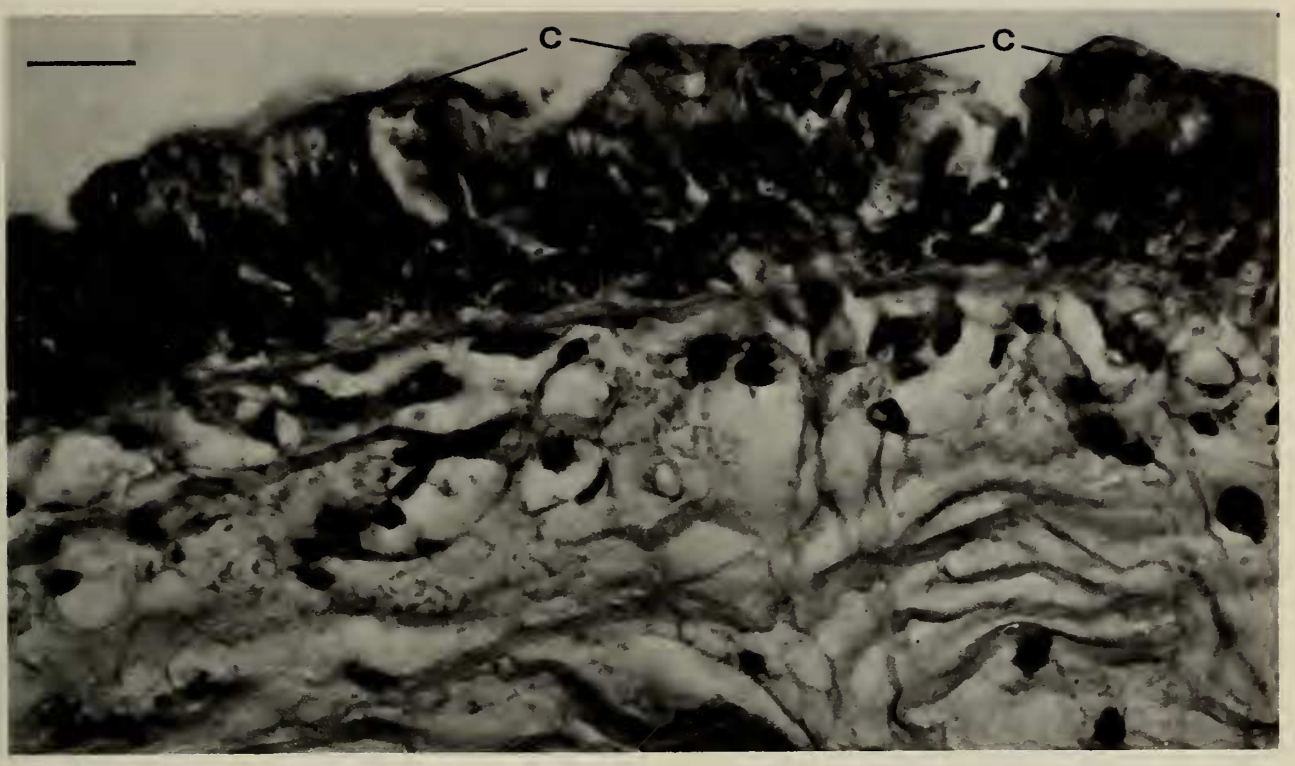


Fig. 6. Epidermal cross section from dorsal surface of caudal region of *Lutodrilus multivesiculatus*, scale 10 μm. **c**, extra-epidermal capillary.

d) Nephridioparietal vessel. Two efferent vessels, 1 each from the lateral body wall and from the nephridium, join near the commissural vessel to form the nephridioparietal vessel.

e) Dorsal septoparietal vessel. The dorsalmost efferent trunk emptying into the commissural vessel is the dorsal septoparietal vessel, which crosses the dorsal septum. This vessel originates in the dorsolateral body wall and receives septal vessels as it traverses the dorsal septum.

Two pairs of dorso-intestinal vessels, equally spaced between septa, arise from the dorsolateral portion of the intestinal blood sinus and extend dorsomedially to the dorsal vessel, which they join on its ventrolateral aspect. These vessels also receive smaller vessels that drain the gut surface. There is an extensive submucosal vascular sinus in the typhlosole, from which numerous vessels convey blood to the ventrum of the dorsal vessel.

Ventral vessel.—This vessel is suspended in the medial mesentery between the intestine and the nerve cord. A pair of ventrotegumentary vessels and 2 or 3 unpaired ventro-intestinal vessels leave the ventral vessel segmentally. Ventrotegumentary vessels, arising in midsegment, penetrate the posterior septum, bifurcate, and then branch to supply the nephridium, posterior septum, and body wall. There are 3 ventro-intestinal vessels per segment, decreasing to 2 posteriorly, where the segments are narrow. The ventro-intestinals arise from the dorsum of the ventral vessel and move dorsally through the mesentery to the vascular sinus of the intestine.

Subneural vessel.—This tiny vessel, located within the neural sheath,

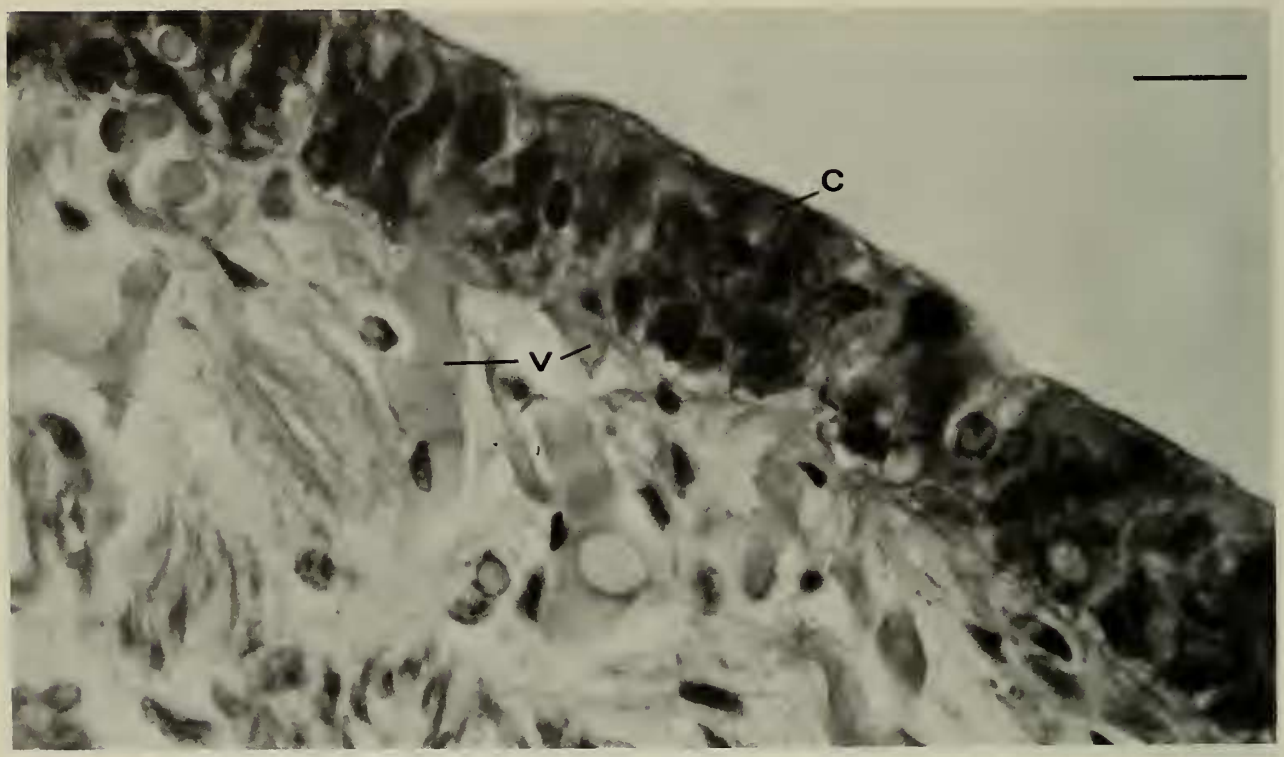


Fig. 7. Epidermal cross section from dorsal surface of caudal region of *Lutodrilus multivesiculatus*, scale 10 μm. c, extra-epidermal capillary; v, blood vessel entering basal layer of epidermis.

capillarizes the nerve cord and has 1 pair of parietal branches per segment.

Pre-periproct Segments.—Near the posterior extremity of the animal, the dorsal vessel receives a pair of commissures comparable to those found further anteriorly, draining the parieties and nephridium of each segment. In addition to 2 ventro-intestinal vessels, the ventral vessel gives rise segmentally to only 1 pair of vessels, which vascularize the septum, parieties, and intestine. The subneural vessel gives rise to a pair of nephridial vessels in each segment in addition to vascularizing the nerve cord.

The 3 longitudinal trunks extend nearly to the anal area, where they capillarize to supply the parieties. Extensive parietal vascularization is pronounced dorsally, and capillaries infiltrate the epidermis, frequently forming subcuticular capillary beds (Figs. 6, 7). Such extra-epidermal capillarization is unknown in other megadrile taxa. There also is extensive vascularization of the intestine, forming sinuses that often constitute one-third of the intestinal wall.

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